STRANGE WASPS INDEED
SPECULATIONS ON THE EVOLUTION OF EUSOCIALITY IN ANTS

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ABSTRACT

Following review of formicid characters a new model for evolution of ant eusociality is presented. This “semisocial ancestry hypothesis” has the following steps: (1) Ants are descended from a solitary wasp which accumulated and collectively reared its brood in acellular nests (without individual brood cells). Metapleural glands delivering antibiotic compounds evolved in adults as a correlated adaptation for nest sanitation. (2) Such wasps gathered to form cooperating family groups of congenerational alate females and their offspring. (3) Female dealation evolved, correlated with pedestrian foraging. Colonies now comprised coeval dealate females rearing alate daughters and sons. Competition generated reproductive and non-reproductive castes in the parental generation, resulting in semisocial colonies, eventually with one dealate mated reproductive queen per nest, and a force of congenerational non-reproductive dealate “workers”. These semisocial formicids progressively acquired petiolar nodes, elbowed antennae, increased longevity and ant-like larvae. (4) Eusociality began when daughter females dealated prematurely and joined the parental-generation worker force. (5) Daughter (eusocial) workers adaptively superceded parental-generation (semisocial) workers and, with the evolution of mechanisms for caste determination, lost mesosomal complexity to constitute eusocial colonies like those of modern ants, with alate/dealate female reproductives and mesosomally-reduced daughter workers. (6) Some of these gave rise to modern ants. (7) Competition between eusocial and semisocial formicids resulted in extinction of the latter, leaving eusocial ants transcendent.

These events occurred early in formicid history. The fossil record indicates that eusocial ants referable to several modern subfamilies were present by late Cretaceous times.

The semisocial formicids could have included derived species either with morphologically undifferentiated apterous mesosomally-reduced females, or with alate/dealate queens and congenerational apterous workers. The extinct upper Cretaceous *Sphecomyrma freyi* is possibly the female or worker of one of these.

It is proposed that the worker caste in modern ants has evolved more than once, and that eusociality arose several times in the semisocial ancestral group, producing separate lineages of eusocial ants, several of which survived to constitute the modern fauna.

The unusual reproductive biology of the aberrant ponerine genus *Diacamma* is reviewed.

Key words: *Diacamma*, Formicidae, Hymenoptera., Sociality, *Sphecomyrma*.

INTRODUCTION

Ants are classified in the family Formicidae assigned to suborder Apocrita of order Hymenoptera. Within Apocrita they are allocated to superfamily Vespoidea. The several other vespoid families comprise the "true" wasps. Three apocritan superfamilies, Vespoidea, Chrysidoidea and Apoidea, are referred to collectively as aculeates. Superfamily Apoidea includes bees and sphecid wasps. This classification represents ants as specialized vespoid wasps.

This essay reviews salient characteristics of the Formicidae, especially their synapomorphies. It considers the evolutionary origins and adaptive features of relevant characters and the possible sequence of their phylogenetic acquisition, their possible evolutionary interactions, the possible effects of each on options for future evolution, and their roles in the evolution of formicid sociality. Some propositions are new to the scientific discussion of ant evolution. It is hoped that they might encourage further discussion and research.

Nomenclature here follows Bolton (2003). "Ponerinae" (with quotes) or "Ponerinae *sens. lat*." refer to that subfamily in the sense of the previous Emery/Wheeler classification. Bolton's terms "mymeciomorph", "poneromorph" etc, refer to sets of putatively related subfamilies. The words "formicid" and "formicids" refer to taxa which have contributed directly to ant phylogeny. The term "standard reproductives" refers to alate females which later dealate (these are also referred to as alate/dealate females).

Many general statements about ants are not been referenced below. They are well covered by Wilson (1971) and Hölldobler and Wilson (1990).

Symplesiomorphies of the Formicidae

Several prominent symplesiomorphies of ants are synapomorphies of order Hymenoptera. Thus (1) sex is genetically determined by haplodiploidy (males haploid and impaternate, females diploid) as in all Hymenoptera (Crozier and Pamilo, 1996), (2) ant mouthparts, apart from the labrum and mandibles, form a labiomaxillary complex with an associated infrabuccal pouch, and (3) mature ant larvae, prior to pupation, enclose themselves in cocoons of silk spun from their labial glands (the many formicid exceptions result from repeated secondary loss of this character).

Other formicid characteristics are synapomorphies of suborder Apocrita: (4) The first true abdominal segment is fused with the thorax to constitute the propodeum, configuring a novel 4-segmented thoracic tagma, the mesosoma, and (5) a deep constriction separates the propodeum and the second true abdominal segment forming a waist between the mesosoma and the segmentally reduced abdomen (termed the metasoma). A small anterior exoskeletal section of the first metasomal segment forms a ball-joint within the propodeum. This facilitates rotation of the sting-bearing metasoma. The operative musculature is largely in the propodeum. Abdominal articulation from the metathorax would be compromised by its leg-bearing function, hence the propodeum has evolved.

Some symplesiomorphies of ants are synapomorphies of the aculeate Apocrita. These include (6) modification of the ovipositor to function as a venom-injecting sting, (7) apodus larvae, and (8)(probably) antennae primitively with 12 articles in females, 13 in males.

Further putative formicid symplesiomorphies relevant here are: (9) ocelli present, (10) a univoltine life cycle with one new generation produced each year, (11) sperm in mated females retained in the spermatheca and used to fertilise eggs for long periods following mating, (12) adults are liquid feeders, (13) larvae are entomophagus, (14) females collect prey to provision larvae, (15) prey is delivered to brood whole, without dissection, (16) males take no part in the lives of females or offspring following copulation, and (17) navigation is visually mediated. The points of phylogenetic origin of these attributes in formicid evolution are less obvious than for those features mentioned previously. All are acceptable as putative formicid symplesiomorphies (Carpenter, 1991).

Formicid synapomorphies

Synapomorphies are the particular features by which we recognize and characterize groups of organisms. The truly homologous synapomorphic characters of any taxon are represented nowhere outside that taxon. Also, where several synapomorphies are recognized, any one of them, on its own (with due recognition of its tansformations), can distinguish a subject taxon from its sister taxa.

Putative formicid synapomorphies relevant here include: (1) female antennae elbowed, with an unusually elongate basal segment (the scape), (2) wing bases in reproductive females structured to facilitate wing-shedding (the action “dealation”, the process “allectomy”), (3) presence of a permanently apterous (wingless) non-reproductive worker caste, (4) metapleural glands present in both adult sexes, (5) first metasomal segment (2nd true abdominal) forming a posteriorly constricted waist node, the petiole, and (6) nests acellular, without individual brood cells. (See Bolton, 2003, for other formicid synapomorphies).

Synapomorphic character states are uniquely and separately acquired in phylogeny. It follows that when several synapomorphies are recognized within a taxon they would usually have arisen in temporal evolutionary succession. The succession can, nonetheless, be so rapid that sets of characters may appear almost simultaneously in phylogeny when organisms are adapting rapidly to extreme selection pressures. Indeed, separate adaptively-related characters probably arise in concert under some circumstances (this might have been the case with co-evolution of acellular nesting and metapleural glands in ants – see below).

The first appearance of each eventual synapomorphy as a newly evolved character would often represent some sort of adaptive break-through, contributing to relative success and diversification of the newly equipped species. Acquisition of a further such character in the accumulation of a set of successively derived future synapomorphies, being a unique event, could occur in only one of the lineages within the subject clade, leaving the remainder as a paraphyletic rump exhibiting the first acquired character but not the second.

Thus, the evolutionary history of acquisition of the formicid synapomorphies listed above must have involved a chain of successive steps, in which taxa equipped with newly evolved characters survived, while their sister groups lacking those characters did not. This process must have been repeated at least often enough to match the number of character acquisitions, and the loss of sister groups must have been complete at each step – how else could so many characteristics of modern formicids be considered synapomorphies. In effect a group possessing multiple synapomorphies could have not just one common ancestor, but a chain of common ancestors, and its lineage might have historically experienced a sequence of extreme diversity bottlenecks.

Characters homoplasious (evolved convergently, and analogous but not homologous) with any of the synapomorphies recognized in a current natural taxon would occur only in separate taxa. These would lack some or all of the remaining synapomorphic character set

Importantly, the most recently acquired apparently synapomorphic character observed in a contemporary taxonomic group could in reality comprise a set of successfully deceptive homoplasious characters separately evolved in the immediately ancestral stock. This is much more likely than with previously evolved characters. We will revisit this proposition below.

Characters resembling most of the above formicid synapomorphies and symplesiomorphies are present as homoplasies elsewhere in nature. Examples include haplodiploidy, production of pupal cocoons, elbowed antennae, univoltinism, visual navigation etc. This is to be expected, and does not diminish the arguments presented here.

Metapleural glands – the classic formicid synapomorphy

Metapleural glands are characteristic of family Formicidae. No antecedent or similar structures are known in other taxa. Their absence in several genera, e.g. *Oecophylla*, *Dendromyrmex*, *Polyrhachis*, most *Camponotus* (not *C. gigas* (Taylor, 1992) and at least two other species (S.O. Shattuck & G.D. Alpert, pers. coms)) and various males (perhaps those of the majority of ants) is clearly due to secondary loss (Brown, 1968; Hölldobler and Engel-Siegel, 1985). Their cuticular components can often be clearly discerned in fossils. Wheeler (1928: 112) first drew attention to the presence of metapleural glands as a character defining the Formicidae.

The glands are bilateral, situated posterolaterally on the mesosoma. Each has an accessory cuticular chamber, usually marked by an external swelling, with a small opening to the exterior. Internally a specialized section of the inner chamber wall receives unicellular ducts from a cluster of relatively large cells lying in the body cavity immersed in haemolymph (Hölldobler and Engel-Siegel, 1985). The structure is almost uniform throughout the Formicidae, with the specialized section of chamber wall usually a flat sieve-like disc, but in *Nothomyrmecia*, *Myrmecia* and some other ants a microperforate vermiform cuticular collecting sac receives the cell ducts, the cell mass is relatively large and the cells relatively small (pers. obs.; Tullock et al., 1962; Hölldobler and Engel-Siegel, 1985)). There seems no reason to doubt that metapleural glands were uniquely evolved and are a genuine formicid synapomorphy.

The glandular fluid contains antibiotic molecules which are proof against various soil bacteria and fungi (Beattie et al., 1986; Veal, Trimble and Beattie, 1992; Mackintosh et al., 1995). Its function is clearly protection of ants, especially their larvae, from contamination or infection. Adult ants groom more actively than other aculeates, and this spreads metapleural gland secretion on their bodies and elsewhere in the nests. The gland does not manufacture the chemicals it secretes, but extracts them from the haemolymph. Some of the compounds involved are found in other insects as components of defensive arrangements equivalent to, but very different from, the vertebrate immune system (Kaaya, 1993; Casteels,1998).

Metapleural glands are important in the social biology of ants. Their adaptive significance is obvious, and their first appearance was doubtless profoundly significant in ant evolution

The powerfully antibiotic metapleural gland secretions are lethal to pollen grains. This explains why ants are barely involved in pollination of flowering plants, and why many flowers are adapted to exclude or repel ants (Beattie et al., 1986). While the acquisition of metapleural glands was a major step in ant evolution, the prospect of a formicid role in pollination was simultaneously closed. Pollination is, of course, a prominent activity among other aculeates, especially in bees

The acellular nest as a synapomorphy of family Formicidae

Various taxa of non-formicid aculeates form reproductive social groups ultimately comprising colonies of one or several coeval females with their brood and adult offspring. There is sometimes also a non-reproductive, exclusively female worker caste. Colonies are typically housed in nests ranging from simple excavations to elaborate constructions. Many of the between-group similarities seen in aculeate sociality and nesting behavior are homoplasious.

Comparative studies of living aculeates with varying levels of sociality and nest complexity reveal that both features are derived ultimately from stocks in which solitary, winged, mated non-social females excavated and provisioned simple nests, each accommodating a single offspring. As more offspring came to be assembled in nests they were, apparently from the beginning, typically housed in separate individual brood cells constructed by the parental females, even when only two or three immatures were involved. Aculeate larvae are primarily entomophagous, and the likelihood of cannibalism among ravenous larvae clustered in undivided nest chambers with immobilized prey is thought to explain the initial adaptiveness of larval segregation. Isolation of individual larvae in such “cellular” nests would likely also impede the spread of infectious disease vectors and parasites, and reduce the risk that all of the brood would be lost in a predatory attack.

Modern nests, no matter how elaborate, are indubitably cellular in virtually all non-formicid aculeates – specifically constructed to segregate each developing individual from its siblings. Cellular nests are remarkably persistent in relevant lineages, and the structural integrity of nests with sections assembled from close-packed hexagonal cells providing strong architectural elements has contributed to the evolution of large, intricate nests such as those of the honeybees and vespine wasps.

On the other hand, the colonies of all ants reside in continuous nest spaces, which house the various brood stages in company with resident adults. The nest space is often a simple chamber, but it may be elaborately divided; either randomly, as when colonies nest in leaf litter; or structurally, as when large nest mounds contain numerous interconnected chambers. Brood is often sorted in stage-specific groups, but no ant is known to house individual immatures in individual cells equivalent to those of other aculeates. Ant nests are “acellular”.

Accommodation of brood in continuous nest spaces is rare among aculeates. Reported examples in solitary sphecid wasps (three species in subfamily Sphecinae, one each in Larrinae and Crabroninae)(Krombein, 1967) are barely exceptions. Loosely partitioned cells are constructed successively in restricted linear spaces by parental females, and chambers with several larvae result when partitions are omitted or later break-down. Krombein reviewed three related *Isodontia* species (Sphecini) “one of which makes individual cells, another with a single brood chamber but sometimes with individual cells, and one which always makes a single brood chamber".

Females of the solitary bee *Megachile policaris* provision individual brood chambers (of which there may be several) with a pollen mass in which eggs are laid, eventually producing a congregation of larvae. According to Krombein this species "differs markedly from other known megachilid bees and, in fact, from almost all aculeate Hymenoptera in that several larvae develop amicably in a single large brood cell with no apparent cannibalism". All species of *Lithurgus* (Megachilidae) have similar behavior (C.D. Michener, pers. com.). Bumble bees (Apidae: Bombini) lay up to 16 eggs in distendable cells. The larvae congregate initially, but later separate themselves with silk partitions (Michener, 1974).

Colonies of the incipiently eusocial allodapine bees (Xylocopinae: Allodapini) and their brood are housed, like ants, in acellular nests. These frequently occupy the slender tubular pith cavities of herbaceous plants or other similar spaces, where the accommodation of numerous individual brood cells would be physically constrained. The adaptive rationale for these nesting arrangements is clear. Allodapines are believed to be descended from ancestors which constructed loosely partitioned cells not unlike the sphecids discussed above. Their acellular nests are to that degree a secondary development. In evolutionary terms the loss of brood cells occurred in correlation with the development of novel nesting arrangements whereby otherwise inaccessible tubular spaces were able to provide accommodation for populous colonies (Michener, 1974). Acellular nesting is an allodapine synapomorphy acknowledged to have arisen uniquely from ancestral stock. Its origin establishes a single exception to the aculeate norm (M.P. Schwarz, pers. com.).

These putative exceptions all involve descent from stock with few larvae and little evident commitment to cellular nesting. There is no evidence of reversals from cellular to non cellular nesting among architecturally more advanced aculeates, suggesting that cellular nesting behavior might be functionally irreversible, particularly when nests are substantially complex.

The above considerations imply that cellular nests might never have featured in the ant lineage (or were never developed to a level precluding evolutionary reversal). Formicids are therefore likely to have originated from a solitary flying wasp which accumulated its larvae in a single nest space without cellular partitions. This behavioral acquisition marked the inception of the formicid phylogenetic clade, and the acellular nest has persisted through millions of years to stand eventually as a synapomorpy of the family Formicidae.

The existence of ants today could have depended on the absence of cannibalism in the larvae of that ancestor. Evolution is like that – very chancy! There would, of course, be extreme selective pressure against larval cannibalism once such nesting arrangements were established.

The earliest formicids

The first formicids would, by virtue of their ancestry, have displayed haplodiploidy; a labiomaxillary complex; ocelli; a propodeum, constricted waist and venom-injecting sting. Adults would have used liquid food and fertilized their eggs with spermathecally-stored sperm. They would have practiced general brood care and foraged for insect or other similar prey returned to the nest as larval food without dissection. Reproduction would have been univoltine, the pupae enclosed in cocoons, and brood overwintered in the nests, probably as larvae. There would be strong selective pressure for overwintering by adults in nests, which would provide protection for hibernating brood. Navigation would have been visually mediated.

The proclivities of modern ants imply that nests would have been constructed in the soil, and that mature larvae within the nests would have been banked with soil by workers prior to spinning their pupal cocoons (as in *Nothomyrmecia*, *Myrmecia*, *Amblyopone* and other “primitive” ants). Observations on living solitary wasps indicate that foraging would likely have been epigaeic and diurnal, with the prey encountered above ground, on vegetation and other exposed surfaces, but not retrieved from within the soil, leaf litter or fallen rotting wood.

The brood would be less protected from disease or fungal infection than in cellular nests. For this reason the evolution of a precursor to the metapleural gland, capable of antibiotic delivery, is likely to have occurred in close correlation with acellular nesting. The near uniformity of metapleural gland accessory cuticular structures implies that the glands would probably have rapidly developed to resemble the modern organs. Recognition of early gland developmental stages might be difficult in fossils because the cells would probably have opened minutely to the body surface prior to evolution of cuticular reservoir chambers.

Cooperation of two or more females in nest foundation, egg laying, brood care, nest defense and foraging would improve brood protection, since the nest could be permanently guarded. Communal aggregation would also support evolutionary increase in colony populations and reproductive productivity, and have an additive effect on efficiency of biocidal protection from metapleural gland secretions, supporting increased nest size. Aggregation would almost certainly have been selectively favored. It would have assembled “primitively social” “polygynous family groups”, as discussed by West-Eberhard (1978).

The evolution of progressive provisioning of the brood would occur as a consequence of the association of adults and larvae in nests. This behavior is found elsewhere among vespoids only in some highly social Vespidae – all other vespoids aside from ants are mass-provisioning (J.M. Carpenter, pers. com.).

Joint colony foundation (pleometrosis) by recently mated females is practiced today by *Nothomyrmecia*, some *Myrmecia* species and other ants (Hölldobler and Taylor, 1983; Wheeler, 1933, Wilson, 1971). The characteristics of this behavior might be homologous with those of the ancestral nesting arrangements hypothecated here.

The ancestral formicids would have generally resembled modern, flying solitary aculeate wasps, except that they would have possessed metapleural glands or antecedent structures.

The univoltine life cycle, brood synchronicity and longevity

Aculeates are generally univoltine, producing one brood each year. Eggs are usually laid in spring. Adults are short-lived, few surviving more than about a year. In most cases colonies die out each winter, with only a few individuals surviving in hibernation to continue the cycle the following spring. In advanced species these are mated females, often found claustral in excavated or preexisting hibernacular cavities (Evans and West-Eberhard, 1973). Overwintering as prepupae or cocoon-enclosed adults is practiced in solitary taxa or those with low levels of social development (Krombein, 1967).

Constructed nests may be perennial but most species construct new nests each year. Reuse of nests is not common, even in socially advanced groups like polistine wasps (Matsuura and Yamane, 1984). In a few cases, mainly in the bee subfamily Apinae, nests are occupied at all seasons by queens, workers, and brood, with in-nest hibernation in areas of severe climate. Even in these, adults are not long-lived and few individuals apart from queens, which tend to live longer than workers, survive more than one active season (Michener, 1974).

Extreme longevity has been frequently reported in queen ants, and workers may survive for several years at least (Hölldobler and Wilson, 1990). Thus at some point in the ant lineage selection favored increased longevity, probably among the semisocial formicids hypothecated below.

There is a general misconception that egg-laying by queen ants is continuous and that all brood stages are present in ant nests at all seasons. Even the writings of myrmecologists can indicate a lack of understanding that ants are primitively univoltine and that the life-cycles of all ants are derived from univoltine ancestry.

Univoltinism is a significant trait of ants. It is demonstrated in colonies of the Australian bulldog ant *Myrmecia gulosa* (Myrmeciinae), in which queens lay eggs for a period of only a few weeks each spring. As hatching proceeds eggs are progressively replaced by small hatchling larvae until only larvae remain. They grow throughout summer and autumn and overwinter as large, incompletely grown individuals. The following spring larval growth resumes and mature larvae begin to spin cocoons. This occurs at about the time egg laying is again initiated to produce the following generation. Emergence of callow adults from the cocoons is complete by early to mid summer. Overwintering larvae do not feed (and might be diapaused, though this has not been investigated), and the workers cease foraging for insect prey during winter, when they seldom depart the nests (pers. obs.).

Transformation of this life history has been frequent among ants. *Myrmecia tarsata* does not overwinter brood. Eggs are laid in spring and emergence complete before the following winter. During winter larvae are absent and foraging for larval food unnecessary. The nest entrances are then sealed with soil, enclosing the overwintering broodless colony. Other *Myrmecia* species seem to be bivoltine, producing a “fast” summer brood maturing in late summer from spring-laid eggs, and a “slow” overwintering brood maturing in spring from eggs laid the previous summer. A survey of the brood contents of many preserved colony series of Australian *Sphinctomyrmex* species (Cerapachyinae) has demonstrated that they overwinter no brood (pers. obs.).

There is evident seasonal synchronicity of brood in the nests of most ant colonies encountered in the field. Winter nests of many species contain only large larvae, while in spring eggs, hatchling larvae and pupae are present. This applies to a range of taxa in both temperate and tropical habitats. *Dacetinops* species in Borneo and lowland New Guinea are typical (Taylor, 1985). These observations imply that the univoltine life cycle with overwintering larvae is common among modern ants. Despite literature search I am unable to say with certainty whether the queens of any ants at all are continuous egg layers. Reporting of seasonal brood contents in ant nests has been inadequate for such analysis

Ant taxa with unusual derived life cycles include the North American primitive formicine *Prenolepis imparis*. It has a seasonally reversed univoltine life cycle, with actively foraging workers and feeding larvae in winter and summer closure of the nests (Tschinkel, 1987). The Australian formicine genus *Myrmecorhynchus*, judging from its winter foraging activity, could be similar.

The so called “Schneirla cycle” of ecitononine and aenictine army ants involves a number of brood cycles each year, and these ants are multivoltine. Brood development is highly synchronized in each colony, and cycles of colony migration are correlated with developmental status of the brood. If the brood events of a single Schneirla cycle are represented on a clock diagram and compared with a similarly derived diagram of the annual cycle of a univoltine ant like *Myrmecia gulosa* the two figures are almost identical, except for their time scales, one of about 6 weeks duration, the other of 12 months. It seems likely that this multivoltine system originated by temporal compression and repetition of the annual life cycle of a univoltine ancestor. The Australian amblyoponine army ant *Onychomyrmex hedleyi* has 3 cycles per year homoplasious with those of the Ecitoninae. The ancestral condition is probably that exemplified by the related *Amblyopone australis*, which is univoltine, with a brood cycle almost exactly resembling that of *Myrmecia gulosa* (pers. obs.).

Univoltine life cycles have almost certainly been the norm throughout ant phylogeny, and the various derived life cycles among living ants probably all evolved following the acquisition of eusociality.

Allectomy as a formicid synapomorphy

Allectomy is a synapomorphy of family Formicidae. Dealation is practiced by fertilized winged female ants after mating and aerial dispersal prior to colony foundation. Wing retention is then no longer adaptive so the wings are discarded and formerly "alate" females become "dealate". Dealation is universal in winged female ants.

Flight for mating and dispersal prior to dealation is clearly adaptive, since wings are developed in the majority of formicid species. Many ants have evolved secondarily worker-like apterous (ergatoid) queens, or the queens have been evolutionarily superceded by mated workers (gamergates)(Peeters and Ito, 2001). These usually mate outside the nests using sexual calling pheromones to attract males, as in *Rhytidoponera metallica* (Hölldobler and Haskins, 1977).

Nothomyrmecia queens have very reduced wings, barely longer than the mesosoma (Taylor, 1978), and cannot fly. These vestiges might facilitate recognition of nubile virgin queens by males. It is likely that some foraging, mated dealate foundress queens and numerous workers would be abroad at the time of mating activity. Mistakes by males in mating with either of these would involve gamete wastage, and would be sociobiologically maladaptive. Also, if queens dealated immediately after copulation this would forestall undesirable supplementary matings. Some species of *Myrmecia* have similarly vestigial wings (Clark, 1951).

Allectomy is rare elsewhere among Hymenoptera. The only reported examples appear to be in the parasitic genera *Leaiopria* and *Mimopria* (Proctroproidea: Diapriidae) which are parasites of termites (Naumann and Masner, 1985). Females shed their wings upon entering established termite nests after flight from parental termitaria. The wings are used for dispersal (and perhaps in mating flight), but are no longer functional in the confines of host termite colonies, so they are discarded. The adaptive rationale is clear.

Allectomy in the ant lineage could have evolved only in females of stock which, though winged, had largely or fully dispensed with flight while foraging, and were therefore already capable of successfully provisioning their nests on foot. This important truism seems seldom to have impressed myrmecologists, who have usually assumed that dealation first evolved because wings would be obstructive in confined nest galleries (as in the aforementioned diapriids). This might be true, but established prior pedestrian foraging would be necessary in any case. The primary adaptive function of allectomy is more likely related to evolutionary loss through wing redundancy in foraging.

The fossil record and other considerations suggest that ants arose as part of the late Mesozoic radiation of insects following the Gondwanic origin and early diversification of flowering plants beginning in the late Jurassic, about 130 million years ago (Grimaldi, Agosti and Carpenter, 1997; Schultz, 2000). Potential prey organisms, especially relatively sedentary phytophagous insects in dense populations, would have been readily accessible as prey for ancestral formicids during those times (as is the case today with *Nothomyrmecia* and various species of *Myrmecia*).

The proposition that pedestrian foraging would be functional in such circumstances is entirely plausible. If an ant ancestor with biology similar to that reviewed above was able to forage successfully without flight, natural selection would act to favor stocks where wing-shedding was present, and to improve its efficiency. That scenario is accepted here.

Pedestrian foraging, nocturnality and hypogaeic behavior

The model proposed here posits that pedestrian foraging originated in formicid phylogeny as an inevitable correlate of allectomy by mated females, prior to appearance of the "true" eusocial worker caste. This may be considered the single most influential event in ant phylogeny, notwithstanding the acquisition of metapleural glands. Some of the reasons for that assertion relate to the activities of modern worker ants, and will be deferred (since eusocial workers have not yet entered this discussion). Others are appropriate for review now.

The development of pedestrianism positioned the ancestral formicids for two profoundly important further developments in foraging behavior and other out-of-nest activities: (1) nocturnality, and (2) hypogaeic foraging. Both of these assertions are justified by biological comparison of modern-day ants with contemporary wasps, among which these activities are barely represented.

Nocturnality

The first pedestrian formicids, perhaps alone among their aculeate competitors, had incidentally acquired the capacity to forage nocturnally – a far from trivial event in their evolutionary success. This would have facilitated activity at times when diurnally active potential competitors, predators and parasites were inactive. Predatory success would be greatly enhanced, since nocturnally torpid resting diurnal insects would be relatively easily captured.

Nocturnal activity is frequently observed among modern epigaeic ants. In many habitats foragers are far more common and diverse at night than in the day. Diurnal activity levels can be high in many habitats, involving an array of species. Suites of other species are abroad at night, with diversity and biomass almost always exceeding those of the day. Ants of many genera like *Nothomyrmecia*, *Myrmecia*, numerous Ponerinae *sens. lat.,* Myrmicinae like *Meranoplus* and *Podomyrma*, and many reported dacetines, are nocturnal epigaeic foragers. Numerous formicines like *Myrmecorhynchus*, *Notostigma* and many *Polyrhachis* and *Camponotus* species are also nocturnal. Colony migration and foraging in the various taxa of army ants is an almost entirely nocturnal activity. In these characteristics ants stand in strong exception to other aculeates.

Nocturnal foraging is prominent in only two vespid wasp genera, the neotropical *Apoica* (Polistinae - with 9 species) and the S. E. Asian *Provespa* (Vespinae - with 3 species)(Schremmer, 1972; Matsuura, 1991). These are proportionately large-eyed compared to relatives, and their nocturnality is crepuscular and otherwise dependent on moon light. They appear to have no special adaptations for this life style, apart from extended visual acuity, and explosive departure of foragers from nests at dusk in *Apoica* (Hunt, Jeanne and Keeping, 1995)(a phenomenon also observed in *Nothomyrmecia*). Both genera are sister to diurnal relatives. Nocturnality is a synapomorphy in each, so only two evolutionary events were required to originate their unusual behavior.

Nocturnality is also exceptional among bees. Species of *Caupolicana* (*Zikanapis*)(Colletidae) have enlarged ocelli and fly when the moon is out. *Lasioglossum* (*Sphecodogastra*) *texanum* is crepuscular but requires flight on moonlight nights to obtain sufficient pollen for cell provisioning (C.D. Michener, pers. com.). Species of *Megalopta* (Halictidae: Augochlorini) and *Perdita* (*Xerophasma*)(Andrenidae: Panurginae) are night-flying, and the former genus includes a subgenus of nocturnal cleptoparasites, *Megalopta* (*Noctoraptor*)(M.S. Engel, pers. com.).

The repeated evolution of nesting behavior among the aculeate Apocrita required the correlated development of precise navigational capacities. Female aculeates have the ability to depart from and navigate back to their nests. Research demonstrates that their navigation is almost exclusively visual, and apparently for that reason overwhelmingly diurnal. Chemical navigation using scattered scent marks is present in some winged species as an unusual exception not necessarily correlated with nocturnality (it is used for example in tribe Epiponini (swarm founding Polistinae) during colony foundation – J.M. Carpenter, pers. com.).

Nocturnal visual navigation by winged aculeates must be sufficiently difficult that it has seldom evolved in flying, nest-building species. Some parasitic wasps fly at night, but they have no requirement for precisely navigated return flights, and within appropriate habitats their flights and resting stations are essentially random.

Visual epigaeic navigation derived from wasp ancestry is clearly the ancestral condition in ants. Much has been written on the subject. The classic study of Wehner, Harkness and Schmid-Hempel (1983) is a well-referenced source. Such navigation by pedestrian epigaeic ants at night, using local landmarks over relatively short distances, is clearly more easily effected than its equivalent in flying visual navigators. It is the modus operandi of *Nothomyrmecia macrops*, of several observed *Myrmecia* species, and many other ants (Taylor, 1978; Hölldobler and Taylor, 1983).

Unpublished field experiments involving canopy manipulation or screening, and the removal or duplication of local tree trunks, demonstrate that *Nothomyrmecia* navigates visually, using the overhead tree canopy silhouetted against the night sky as a map. Similar canopy navigation occurs in the African ponerine *Paltothyreus tarsatus* (Hölldobler, 1980). There is no detectable evidence that *Nothomyrmecia* uses scent trails.

In conclusion it is clear that the aculeate night belongs to the ants, and that the correlated evolution of pedestrian foraging and nocturnality greatly advanced evolutionary success in the formicid lineage.

Hypogaeic foraging

Hypogaeic foraging involving the search for prey in the soil or leaf litter, in or under rotting wood lying on the ground, or under stones, is rare among winged vespoid or sphecid wasps. It is, however, the usual predatory mode of numerous ant species, some of which are so deeply committed bionomically to life underground that they are seldom observed abroad, even on the soil surface. Such hypogaeic elements are typified by most Amblyoponinae and many (but not all) species of the other poneromorph subfamilies, the dorylomorphs, leptanillomorphs, and some myrmicines. Their prey includes an array of soil-dwelling animals (mainly arthropods), often including eggs or larvae. The distinction between nocturnal and diurnal activities seems not to be significant in the most hypogaeic of these species.

Alternatively, several major ant lineages predominately include epigaeically foraging species. These seek prey largely on vegetation or the ground surface, without penetration or excavation of soil, litter or rotting wood. Many of them are nocturnal They include the myrmeciomorph subfamilies Myrmeciinae and Pseudomyrmecinae, all species of which are epigaeic, and the formicomorph subfamilies Dolichoderinae and Formicinae, most of which are epigaeic.

The prey of vespoid and sphecid wasps rarely includes specialist soil-dwelling animals (Krombein, 1967). These insects hunt epigaeically, usually on vegetation, or on the ground or other exposed surfaces. Soil-dwelling arthropods, such as subterranean insects and their larvae, or subsoil-inhabiting spiders and centipedes are seldom encountered, if at all.

These distinctions between ants and wasps appear to be related to the presence of wings in foraging apterous aculeates, and their absence in foraging ants. It may reasonably be surmised that penetration of the soil, litter or rotting wood, and the obstructed retrieval of immobilized prey encountered there, would be maladaptively risky for winged foragers (especially regarding potential damage to their wings), and that this explains the near-absence of such behavior in winged aculeates.

Some groups of parasitic (as opposed to predatory) Apocrita include species with permanently apterous, somewhat worker-ant-like females. Among aculeates these include members of the chrysidoid families Dryinidae, Bethylidae and Chrysididae, and the vespoid families Mutillidae and Typhiidae. Many of these females enter the soil or litter in search of hosts (usually insect larvae), prior to oviposition. The hosts are not usually later withdrawn from cover. The aptery of these species seems likely to be adaptively correlated with this hypogaeic lifestyle. It has clearly evolved convergently and frequently. These exceptions support the assertion that the presence of wings is not conducive to hypogaeic foraging.

The opportunities furnished by the evolution of apterous pedestrianism for the subsequent acquisition of nocturnality and/or hypogaeic foraging activity were clearly variously exploited in later formicid evolution. This is evidenced by the diversity among modern ants with respect to these behaviors. It seems clear that there must have been early separation of lineages, some of which were primarily epigaeic (and frequently nocturnal) in foraging behavior, and others which were primarily hypogaeic predators. *Myrmecia* and *Amblyopone* today exemplify eventual eusocial products of two such alternative groups. Haskins and Haskins (1951) pointed out that these genera represent “widely divergent groups of ants” despite resemblance in many aspects of their colony foundation and general social organization. The differences between them can readily be explained by the present hypothesis that their distant Mesozoic ancestors responded differently to the opportunities associated with pedestrianism - one lineage retaining wasp-like epigaeic behavior, leading to *Myrmecia* (in which many species are also nocturnal) - the other adopting a hypogaeic lifestyle, leading to *Amblyopone*. The similarities between them are primarily derived from their distant common ancestry.

The petiole and elbowed antennae

A posteriorly constricted petiolar node comprising the first metasomal segment (2nd true abdominal) is a synapomorphy of family Formicidae. The large remaining section of the metasoma is termed the gaster. The 3rd abdominal segment often has its tergite and sternite fused or firmly joined laterally. Its anterior part forms a ball-joint enclosed by the petiole (a configuration serially analogous to the propodeal/petiolar joint in Apocrita, and with a similar set of composite structures). The petiole is very narrowly constricted posteriorly in almost all Formicinae and Dolichoderinae, but broadly articulated in some other ants, notably in subfamily Amblyoponinae. The extra articulation clearly increases gastral rotation. Stinging ants probe prey with the mandibles, apparently seeking chinks in the exoskeletal armor. When the jaws find purchase the sting is swung far forwards under the body and applied near the mandibular tips. The eggs of queens, and trophic eggs in workers, are removed from the abdominal tip in similar manner. Venom-spraying formicines like *Formica* spray forwards with the gaster held under the mesosoma (hence the ancient name “pismires”). The grooming behavior termed “abdominal tip cleaning” in which the gastral apex is swung ventrally forwards to the mouthparts might, incidentally, be an ant synapomorphy, apparently absent in other aculeates.

The antennae are elbowed in female ants with the scape notably elongate, often nearly as long as the other articles together. This increases antennal mobility and reach, especially in confined nest chambers. Scape length is functionally correlated with mandibular length, and is considered an adaptation supporting antennation (olfactory scanning) of brood and potential prey, and other workers, as in trophallaxis (Dlussky, 1975).

The non-eusocial, semisocial formicids

This argument has now reached a stage where the pivotal formicid stock hypothecated here has been prescribed. Its species are resident in colonies each comprising a group of coeval dealate, fertilized females, variously and seasonally with their eggs, larvae and pupae, and also seasonally with second-generation alate females and males. The winged virgin adults leave the nests to mate and males afterwards disperse. Newly mated females typically seek potential nest sites by flying and pedestrian search and join with other coeval females jointly to found further colonies. Alternatively, they might enter established colonies (perhaps without first mating) to supplement their personnel, contributing to the development of larger colonies than would otherwise be possible. There would likely be strong adaptive support for this behavior. Dealation in each female occurs after the mating flight, or upon entry to a new nest. It seems probable that the mode of colony assembly would limit the prospects for development of very large colonies, even considering that alternative strategies might be evolved.

Polygynous family groups like the above are common in social bees (Michener, 1974). Twenty nine sphecoid and vespoid wasp species in which non-reproductive workers are lacking and adult females share nests were listed by West-Eberhard (1978), who estimated the existence of at least 39 such species.

These insects would initially have had wasp-like characteristics, but would become increasingly ant-like as they diversified. Ocelli would initially be present in all individuals, and elbowed antennae and a petiolate waist would be present in some species, though perhaps not fully ant-like. Selection would probably favor increased adult longevity, perhaps to levels like those known in living ants. The larvae would become progressively more ant like, some probably with the crook-neck-squash shape seen in Myrmeciinae and Amblyoponinae. Foraging in many species would be nocturnal, with dealate pedestrian foragers and visual navigation.

Comparative research on social wasps and bees demonstrates that reproductive competition between the parental females in such communal nests would result in the evolution of more-or-less morphologically undifferentiated reproductive and non-reproductive female castes, even (in the early stages) if the non-reproductives had mated. Also, some virgin females might dealate without mating to become workers. The resulting social arrangements (with 1-generational matrifilial colonies, a worker caste and division of labor) are defined as “semisocial”. These would be “caste-containing groups” in the sense of West-Eberhard (1978).

The asymmetries of relationship between the parental and daughter generations, related to haplodiploid sex determination (which will not be explored here), would selectively favor the presence in each colony of a single mated reproductive individual, the Queen.

It will be argued below that this pre-eusocial stage would likely have been temporary in ant phylogeny, but its significance would have been profound because, among other things, it would have facilitated the evolution of efficient behavioral relationships and communication between cooperating workers and between larvae and workers. Most importantly for this model, these would include the communication of hunger by larvae to workers, in order to stimulate foraging and prey-seeking behavior.

Considering its unique past acquisition of several highly adaptive major characteristics, this lineage of “semisocial formicids” would have experienced great evolutionary success. It would almost certainly have undergone adaptive radiation and taxonomic diversification, possibly with the evolution of many species, genera and even higher taxa. There would be a diversity of general lifestyles and degrees of crypsis in nesting and foraging, preferred nest sites, prey preferences, mating flight parameters, modalities of reproductive behavior etc. The structure of the mandibles in particular would have diversified in adaptive response to requirements for dealing with different prey organisms in different groups, and some taxa would doubtless have specialized on particular types of prey. Adult size would likely vary greatly between taxa. Interspecific competition would be profound, as usual among related, similar species. This would generate biological and ecological displacement and consequent adaptive shifts, which would contribute to further diversification and radiation.

It is likely that some of the hypothecated semisocial formicids would have evolved fully apterous females like those seen in other apocritan taxa (notably in Mutillidae, Tiphiidae and Rhopalomastidae). Thus species with mesosomally-reduced workers and morphologically undifferentiated reproductive females could have occurred. They would in some cases have resembled workers of modern eusocial ants. This evolution could follow if the alate females abandoned flight in mating, and instead attracted males using sexual calling pheromones. The wings would thus lose adaptive function and natural selection would eliminate them. This would probably be an all-or-nothing situation, with females either all standard (alate/dealate) or all permanently apterous, depending on the species.

The evolution of high-level female polymorphism, with congenerational standard reproductives and fully apterous ant-like workers (and appropriate caste-determining physiological or sociobiological processes) would possibly have evolved in some taxa. The main lineage, leading to eusociality must have retained winged females and allectomy, for that is the synapomorphous condition in modern ants.

Untransformed non-eusocial formicids seem no longer to exist, but in evolutionary terms they could well once have constituted a diverse, vigorous group.

Feeding, foraging and larval communication

Adult ants, like those of other aculeates, are liquid feeders. This is reinforced by use of the labiomaxillary complex and infrabuccal pouch to remove large particulate inclusions from the food, and by removal of fine particles from the digestive tract by the proventriculus, which functions as a valve-dam. The proventriculus is variously and elaborately specialized for this purpose among ants (Eisner, 1957)[1].

Ant larvae, however, are primitively entomophagus and feed on the solid masticated flesh of prey (the many exceptions, including graminivory and liquid feeding by larvae, are derived transformations of this character).

Thus, foraging adult ants are motivated by two behavioral drives: (1) to collect insect or other prey for their larvae; (2) to locate and utilize liquid food for personal nourishment.

Unpublished field studies on *Nothomyrmecia* demonstrate that these drives are separately satiated. Nocturnally-foraging workers delayed experimentally at honey baits early in their progress imbibe the liquid avidly. They do not return to the nests when the drive for self-nourishment is satiated, but proceed to hunt for insect prey. Their prey-getting drive is satiated when predation has succeeded, stimulating return to the nest by foragers carrying booty. Otherwise that drive subsides at dawn when numbers of unsuccessful foragers return home.

The self-feeding drive is doubtless activated by worker hunger, but the prey-getting drive might need to be triggered by larvae communicating their need for food to attendant workers, which would be thus stimulated to leave the nest and to forage.

Such arrangements might be indicated by the fact that colonies of various ants are known periodically briefly to cease foraging, later to resume. This is pronounced in the nocturnal *Nothomyrmecia macrops*, where workers from previously active foraging colonies have been observed not to depart their nests on nights when those from adjacent colonies were foraging (and climatic conditions therefore not inimical), and to resume full activity the following night. It is reasonable to suggest that larvae in these resting colonies were then well fed, were not communicating hunger, and thus were not stimulating worker foraging behavior.

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[1] Eisner emphasised those taxa with the most derived proventricular structures (mainly genera of subfamilies Formicinae, Dolichoderinae and Aneuretinae). There is need for further research among the poneromorph subfamilies and those not yet studied. *Amblyopone* was shown to have a uniquely 6-partite proventriculus while all other species studied were 4-partite, including *Odontomachus*, the only other poneromorph reviewed. The two myrmicines and sole doryline examined had "degenerate" proventricular structure, while that of *Cerapachys* (Cerapachyinae) was more complex.

I have frequently maintained and studied colonies of Australian bulldog ants (*Myrmecia*) in observation nests. On several occasions workers which would normally attack introduced live insect prey have completely ceased such activity and ignored potential prey. This occurs following pupation of the last larvae present in relevant nests. The enclosure of larvae in pupal cocoons seems effectively to have removed larval influences, so the workers were no longer motivated for prey-collection.

Authors have suggested that head waving and other body movements might be used by larvae to communicate with workers. The demonstration by Cassill and Tschinkel (1995) of olfactory communication of hunger by larvae to tending adults suggests a much more precise mechanism. It raises the question that this communication might generally be pheromonal. More research is desirable.

The evolution of formicid eusociality

The term "eusociality" refers to the level of social development attained by modern ants. It requires the presence of overlapping generations, extreme division of reproductive labor, and cooperative brood-care by non-reproductive adults. The workers of eusocial ants are not coeval with their queens, but members of the following generation.

The queen (there is usually one per colony) is normally the mother of all other individuals resident in a nest – all eggs, larvae, pupae and adults are her offspring - though males, which are genetically haploid, may sometimes be derived from unfertilized, worker-laid eggs (Crozier and Pamilo, 1996). Reproduction is the queen's prerogative. She is the only member of the colony to have previously mated. The sperm bank on which her reproduction depends is carried in her spermatheca.

The workers are specialized brood-carers, and have in most cases lost the physical capacity for reproduction. The ability to develop wings has been lost in their evolutionary derivation, and the pterothoracic mesosomal sclerites specialized for flight have been deleted or fused, resulting in drastically simplified mesosomal structure.

Eusociality has evolved homoplasiously several times elsewhere in the Aculeata. Classic examples are wasps of subfamilies Stenogastrinae, Polistinae and Vespinae, members of the bee subfamilies Meliponinae and Apinae and the remarkable sphecid *Microstigmus comes*. No other eusocial species have fully apterous workers like those of ants.

Evolutionary transformation of the semisocial formicids posited above to fully eusocial ants would require the daughter females to became non-reproductive workers. These second-generation workers would eventually supplant the phylogenetically antecedent dealate queen-coeval workers. Natural selection would act to favor individuals with diminished reproductive organs and reduced alary and mesosomal complexity, ultimately to produce fully apterous non-reproductive workers with simplified mesosomal structure. Physiological or sociobiological mechanisms effecting caste determination would evolve in concert.

The first step to eusociality would require little more than the presence of unmated dealate daughter workers in nests. If their supplementation of the worker force was adaptive, natural selection would work to formalize the process. The other components of eusociality are already latent in the lineage. Details, such as loss of the dealate queen-coeval worker caste and reduction of worker mesosomal complexity would later be effected by natural selection, to produce all the defining characteristics of modern formicid eusociality.

The hypothecated semisocial formicids can be considered neatly predisposed for evolution of the daughter worker caste. The necessary first step is elegantly simple. It requires premature dealation. There are at least two models by which this could occur:

(1) *The larval manipulation hypothesis*:

All females in semisocial formicid societies, including alate daughters, would inevitably be programmed by evolution with the instincts (1) eventually to perform dealation and (2) to respond to stimulation from hungry larvae by foraging. All that is required is for some daughter alates to respond prematurely to the imperatives of larval stimulation by foraging, and to lose their wings by premature dealation without having mated.

This process can be envisaged as larval manipulation because it would be in the interests of larvae to increase the force of workers dedicated to their care.

(2) *The parental manipulation hypothesis of Alexander (1974)*:

In this case the reproductive female(s) would impose the worker role on alate daughters by forcibly removing their wings, as happens (in effect) in contemporary *Diacamma* species (see below).

In either case, because mating requires flight, dealation of the daughter workers would preclude them from future reproduction. The asymmetries of relationship to their mothers and sisters, occasioned by haplodiploid sex determination (Crozier and Pamilo, 1996), would favor their assumption of the worker role, to assist in the production of reproductive siblings from eggs laid by their fertilized mothers. In this way daughter workers would appear almost instantaneously. Assuming that the arrangement was competitively successful natural selection would rapidly improve the functionality of this newly acquired eusociality.

These scenarios are presented as models for the evolution of formicid eusociality. Dealation is a systematic component, and because of its presence the evolution of eusociality in ants has followed an entirely different course from those hypothecated to have produced eusociality elsewhere among winged eusocial aculeates.

The initial step is so simple that it could be considered an almost inevitable prospect (though certainly not in any way pre-ordained) for formicids with the hypothecated semisocial lifestyle suggested above. Either scenario could easily have occurred more than once in the formicid clade.

Semisocial formicids with standard females and mesosomally-reduced workers, as formulated above, could similarly evolve eusociality. They would have the advantage of pre-existing caste determination mechanisms. Those with monomorphic, fully apterous females would be unable to initiate eusociality, at least not along the lines suggested here.

Did the ant worker caste evolve more than once?

One of the “givens” of myrmecology is that evolution of the worker caste and resultant eusociality was unique in ant phylogeny. This proposition is rarely mentioned, far less questioned (though see Wilson, 1971: 74, for a suggested separate origin of amblyoponine sociality). Its pervasiveness is evident. Consider that every published formicid “family tree” is rooted in assumptions that (1) the ancestor of all ants was itself eusocial, with an apterous daughter worker caste, and (2) all of the diversity of modern ants is derived from that single ancestor, and (3) that its appearance predated the complex evolutionary branching which established the major taxa of ants.

The possibility that the worker caste is not a synapomorphy of family Formicidae, but that workers and eusociality might have been homoplasiously derived more than once from a group of non-eusocial ancestral formicids, seems never to have challenged the entrenched position.

I propose that the worker caste in ants might not be uniquely evolved, but homoplasious. This hypothesis has the following components: (1) that the daughter worker caste and eusociality arose more than once from an ultimately monophyletic but diverse group of pre-eusocial, semisocial, formicids of the kind hypothecated above; (2) that multiple derivation of eusocial workers among the semisocial formicids would have been unexceptional, given the simplicity of such evolution along the lines suggested in this essay; (3) that some of the major features of modern ant diversity were already present among the antecedent non-eusocial formicids and survive today to define some of the major lineages of family Formicidae. Each relevant lineage, according to this model, originated from a taxon within the ancestral pre-eusocial group which had acquired a daughter worker caste and eusociality separately from other such taxa; (4) That the hypothecated non-eusocial formicids, although argued here likely to have been a diverse and successful group, have become extinct as failed competitors of eusocial ants; (5) that the process of worker mesosomal simplification proceeded separately with each acquisition of eusociality and that these separate origins have comprehensively produced deceptively similar worker mesosomal structures across the diversity of modern ants.

It is arguable that myrmecologists have been consistently deceived by the convergences in worker mesosomal structure. As long as the observed reductions were accepted as being homologous the worker caste and eusociality were accepted to be monophyletic. In fact, of course, there is much diversity of mesosomal structure among worker ants.

This hypothesis is posited as a challenge to others to consider, and perhaps to test its propositions and implications. Some further comments are in order.

It implies that the latest *common* ancestor of *all* extant ants was a semisocial wasp-like formicid. It does not challenge the family Formicidae as a natural clade. If accepted it would have little impact on the taxonomic classification of ants, except that some current taxa might be raised in rank if their eusociality is considered to be independently derived. Bolton's elevation of the former "ponerine" tribes Amblyoponini and Ectatommini to subfamilies (the Ectatommini to four: Ectatomminae, Heteroponerinae, Paraponerinae and Proceratiinae) might already have partly accomplished this. Bolton's formicomorph, myrmeciomorph, and leptanillomorph subfamily groups and the subfamily Ponerinae could be separately derived lineages, and the myrmicomorphs might be derived severally from stock shared with the poneromorphs.

Many ants have a second waist node, termed the postpetiole, formed by posterior constriction of the 3rd true abdominal segment, and the related formation of an articular exoskeletal ball-joint anteriorly on the 4th segment. This arrangement seems likely to have been derived more than once.

Greater understanding of the processes of mesosomal reduction and of evolution of the postpetiole is needed to identify cladistically useful characters. Is tubulation or some similar modification of the 4th true abdominal segment a necessary precursor to the evolution of a postpetiolar node and its articular condyle?[2] If so, is this configuration uniquely evolved, and what does the answer to that question say about affinities among the various postpetiolate subfamilies of ants? Brown (1954) recognized separate "poneroid" and "myrmeciioid" lineages. If his treatment of the myrmeciomorph subfamilies (*sensu* Bolton), including the Myrmeciinae and Pseudomyrmecinae, is set aside, Brown's hypothesis basically separates the abdominally tubulate (and frequently postpetiolate) ants from the remainder (i.e. the Aneuretinae, Dolichoderinae and Formicinae). In effect it posits two clades within the Formicidae. Ward and Brady (2003) rigorously estimated that the subfamily Myrmeciinae diverged from other ant lineages about 100mya. That lineage might have been established as a third major clade before it evolved eusociality. This would imply separate evolution of postpetiolar

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[2] The term tubulation (in the sense of Taylor, 1978) refers to the configuration of the 4th true abdominal segment. It is "tubulate" when the lateral margins of its tergite and sternite are aligned and more-or-less fused to assemble a strong cylindrical structure. This is partly inserted into the exoskeleton of the preceding segment 3 to furnish a rotatable joint. The inserted section is set off from the remainder of the segmental exoskeleton by a girdling constriction. When segment 3 constitutes a postpetiolar node the anterior section of segment 4 can be very small, forming a ball-joint articulating the large terminal abdominal tagma (termed the "gaster", but here 1 segment shorter than the formicomorph gaster). This arrangement is an analog of the constricted preceding propodeal/petiolar and petiolar/postpetiolar joints.

structures, as seems likely on anatomical and phylogenetic grounds (P.S. Ward, pers. com.).

Some modern taxa seemingly could have evolved only from eusocial stock. The dorylomorph army ant subfamilies (Ecitoninae, Aenictinae, Dorylinae and Leptanilloidinae) are pertinent. Models for their derivation, culminating with the work of Brady (2003), have consistently implied descent from unexceptional eusocial non-migratory primitive poneromorphs (see Wilson, 1958). Brady's analysis has them sharing ancestry with the Cerapachyinae (which were also placed as dorylomorphs by Bolton, 2003).

The *Diacamma* enigma

The ponerine genus *Diacamma* has social organization strikingly different from those of all other ants. It could be an informative exception, and must be considered in any broad discussion of ant eusociality.

Diacamma is Indo-Australian, with perhaps 30 species. The bionomics of an Okinawan species (the sole Japanese taxon, identified then as *D. rugosum*) were reported by Fukumoto, Abe and Taki (1989). A second species (*D. australe*, Queensland, Australia), with essentially identical biology, was reviewed by Peeters and Higashi (1989). The following account is based on these reports and other research detailed below. The genus typically forms small colonies in surface soil and leaf litter. Its females are uniformly apterous, and there is no *general* morphological differentiation between the sole parental reproductive in each nest and associated workers.

All *Diacamma* females at eclosion carry a pair of tiny bilateral lobate appendages housed in small dorsolateral mesonotal pits, which are considered to be vestigial wings (Tulloch, 1934). Their presence determines reproductive status. Females with appendages are able to function as reproductives, to mate and produce diploid offspring. Those without function as non-reproductive workers. Reproductive status (i.e. caste) is controlled by the parental female removing these appendages from prospective workers as they emerge from their pupal cocoons. In this way vigorous resident reproductives are able totally to prevent their daughters from becoming reproductives.

Colonies reproduce by fission. A group including the parental reproductive and workers departs to establish a new nest. Cocoons containing pupae remain with workers in the original nest. The females eclosing from these compete among themselves to retain their vestigial wings which others attempt to remove. Eventually one (usually the first to emerge) remains intact – she becomes the prospective new reproductive. She leaves the nest to mate nearby after sexually calling a male partner. Following return she begins to lay fertilized eggs. Reproductives alone retain wing vestiges in the nests (i.e. there is no equivalent of dealation after mating). The cycle continues.

Note that the new colony is initially semisocial[3], with the reproductive and workers all daughters of the same female. These ants are clearly eusocial, though with a distinctive caste-determination system, and a major semisocial phase in their colony cycle. If the species was univoltine the semisocial phase could last for almost a year until the first offspring of the new queen emerged.

Both the Fukumoto and Peeters groups demonstrated that reproductives by their presence are able to inhibit the production of haploid (male) eggs by workers (a not unusual trait in queen ants), and both considered their subject species to be “queenless”. Peeters and Higashi identified the reproductive females as gamergates (mated reproductive workers).

The mesonotal appendages were termed “gemmae” by Peeters and Billen (1991) and shown to be highly glandular by Billen and Peeters (1991), who presumed this to be related to “the peculiar mechanism of reproductive regulation found in this queenless ant”. Mesosomal anatomy of *D. australe* was discussed and illustrated by Bitsch and Peeters (1992) who confirmed that the mesonotal appendages were vestigial mesothoracic wings. Gronenberg and Peeters (1993), concluded that workers lacking gemmae can never replace a gamergate. Peeters, Billen and Hölldobler (1992) discovered that the gemmae were not removed in workers of the Indian *D. vagans*, and that mated top-ranked individuals dominated the nests and functioned as reproductives. Similar reproductive dominance occurs in orphaned groups of the Japanese species, with an alpha dominant worker monopolizing haploid egg production (Peeters and Tsuji, 1993). Sommer, Hölldobler and Rembold (1993) described a Malaysian species with bionomics similar to the Japanese model. Following comparison of four Indian species, Veuille et al. (1998) demonstrated that retention of gemmae is the derived condition *versus* gemma removal in *Diacamma*. Recent literature, too extensive for citation here, has shown that other *Diacamma* species have worker castes determined by the removal of gemmae.

There are two possible origins for this remarkable behavior. Either it is primary, derived directly from a non-eusocial ancestor, or it is secondary, derived from a eusocial ancestor. Two possible secondary models are:

(1) That *Diacamma* was derived from a conventionally eusocial ancestor through acquisition of gemmae and associated mesosomal structures by its workers, followed by replacement of the queen caste with gamergates. This seems improbable because gemmae, as wing vestiges, would need to be developed on an already structurally-reduced mesosoma, and it is not easy to understand why this would happen in eusocial ants with a pre-existing caste-determining mechanism.

A shift in gene expression could theoretically reassign “queen” characters to the workers, producing partial resurrection of an unreduced

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[3] This is the case also in all but the first departure in a series of honey bee swarms and presumably in other swarm-founding aculeates, including ants with apterous reproductives and colony budding.

mesosoma and wing vestiges in a lineage formerly with mesosomally-reduced workers. Apart from the possibility that ocelli were restored in this way to the workers of *Harpegnathos* (which are uniquely ocellate among ponerine workers) there seem to be no other examples of this phenomenon in poneromorph ants.

(2) That a secondary round of worker-caste evolution occurred from conventional eusocial ancestry, starting with groups of coeval alate/dealate females, the descendents of which eventually enacted a scenario like that outlined below. Potential startup groups could perhaps originate from assemblies of pleometrotic colony foundresses.

Neither alternative seems very plausible and both models require extinction of conventionally eusocial ancestral stock.

One hesitates to suggest the primary option, but, consider the following evolutionary scenario: (1) A monomorphic alate/dealate semisocial formicid has small colonies comprising congenerational dealate workers and a single dealate reproductive female. They rear alate females and males from eggs laid by the reproductive female. (2) The reproductive female co-opts some of her alate daughters as workers by forcibly removing their wings. Unmutilated daughters are able to fly and mate. They are the future reproductives. (3) The daughter (eusocial) workers adaptively supercede the queen-coeval (semisocial) workers, and the evolving lineage attains eusociality. Worker determination continues to be controlled by removal of wings from virgin alates by the queen. (4) A descendent lineage abandons the mating flight and reproductive females use pedestrian sexual calling to attract males. Wings are no longer adaptive for flight and the lineage moves towards monomorphic aptery, undergoing evolutionary reduction in wing size and simplification of mesosomal structure. (5) The wings are eventually not entirely lost, but tiny lobate vestiges of the forewings remain, housed in small dorsolateral mesonotal pits. Caste is now determined by the parental reproductive female removing these vestigial wings from prospective workers etc.

Of these alternatives the first secondary model seems the least implausible. The second might satisfy those who believe that *Diacamma* females are phylogenetically degenerate queens. The primary model would gain some support if *Diacamma* stood taxonomically apart from other ants, but all relevant cladistic and other analyses place the genus firmly in the subfamily Ponerinae as presently constituted (though this remains a probably artificial group likely destined for more dismemberment such as that by Bolton, 2003). The primary model would not be implausible if the taxonomic difficulties could be resolved. If accepted it would firmly demonstrate that modern ant eusociality evolved at least twice from non-eusocial stock, falsifying the common assumption that it is uniquely derived.

Pedestrianism in eusocial ants

The evolution of worker aptery and pedestrianism expedited both nocturnality and hypogaeic foraging among the semisocial formicids posited here, contributing to their adaptive success. Pedestrianism remains influential among formicids. One of its major advantages is that much larger, heavier, prey can be carried or dragged by individuals than is possible in flight, and foragers can readily cooperate in the transport of large prey.

The evolution of worker subcastes, including large-headed majors or "soldiers" would otherwise be nearly impossible. They are unknown among winged social aculeates, except for Australian halictine bees of genus *Lasioglossum*, which have a caste of large-headed, small-winged males which stay on the nests, fight for possession of females and repel parasites (Houston, 1970). The aerodynamic constraints of macrocephaly seem likely to have constrained its development in winged aculeates. Ants, being pedestrian, suffer no such constraint, and macrocephaly clearly does not inadaptively inhibit progression by large-headed soldiers, which have evolved repeatedly and are present in several subfamilies.

The absence of wings has allowed ants to nest in a diversity of situations barely exploited by flying aculeates.

Permanent substrate contact has occasioned repeated evolution of scent trail-laying techniques important in foraging, nest migration and worker recruitment to food. These utilize a range of chemicals and specialized glands unknown among other aculeates (Hölldobler, 1978, and subsequent papers). Trail pheromones are produced by a rich diversity of glands, and their taxonomic distribution could provide characters useful for phylogenetic analysis.

What happened to the ant ancestors?

The adage "extinction is the common lot, survival the exception" applies to the history hypothecated above. Extinction of taxa related to the crown group is a necessary component at each step in the phylogenetic assembly of modern ants, establishing the status of characters now accepted as formicid synapomorphies.

The pre-eusocial formicids seem unlikely to have been very effective competitors of eusocial ants. Their lifestyle would likely have been less efficient than eusociality. Colony size is probably inherently limited, and potentials for behavioral and biological diversification more restricted than in true ants.

Various ants are known to be highly effective biological competitors of other ants and to locally eliminate other ant species. Consider the success of "tramp" species introduced by human commerce to new localities. They regularly eliminate or restrict resident endemic ants or other introduced species from their habitats. Their overwhelming competitive abilities involve not only ecological success, but direct, targeted violent aggression (Holway et al., 2002). The vagaries of the Argentine ant, *Linepithema humilis* and the Madeira ant *Pheidole* *megacephala* in Bermuda (Haskins and Haskins, 1965, 1988), and the neotropical Little fire ant *Wasmannia auropunctata* in New Caledonia (Fabres and Brown, 1978), Cameroon and the Galapagos Islands are prime examples.

It is accepted here that the hypothecated non-eusocial formicids could have been eradicated by competitive assault from true ants. Similar apocalyptic extinction has not occurred in the other eusocial aculeates. Wasps (with some exceptions like *Vespa*) seem less prone than ants to assault their relatives, and flying adult wasps can more readily escape attack than pedestrian formicids. Even if their brood was lost they could survive, possibly to reestablish their nests. Bees have moved away from larval entomophagy. As pollen collecting herbivores they are not given to attacking other bees. I suggest that for these reasons a diversity of social life-styles ranging from solitary to eusocial has survived among the wasps and bees, but not among ants.

The timing of events

The earliest phylogenetic events posited above would probably have occurred in rapid evolutionary succession following acquisition of acellular nesting and metapleural glands. It is now accepted from fossil and other evidence that eusocial ants first appeared in the Mesozoic perhaps 140-100 million years ago (mya). Their rise by the late Cretaceous is evidenced by several recently described fossils, which demonstrate that eusocial ants of modern appearance, with close modern taxonomic affinities, were present in those times.

The fossil *Kryomyrma neffi* Grimaldi and Agosti (2000a) from late Cretaceous (Turonian) New Jersey amber (estimated 92 mya) is an indubitable formicine worker, with detailed resemblance to modern taxa.

The genus *Afropone* Dlussky, Brothers and Rasnitsyn (2004) with two species represented by compression fossils of late Cretaceous age (Turonian, 93.5-89.3 mya) from Orapa, Botswana was assigned by its authors to subfamily "Ponerinae". Its metasomal structure, with a differentiated postpetiole, is derived when compared to the usual ponerine configuration, and resembles that of the modern myrmeciomorph subfamilies Myrmeciinae and Pseudomyrmecinae, to which *Afropone* could be annectant. Its large eyes support this assignment.[4]

Brownimecia clavata Grimaldi, Agosti and Carpenter (1997)(White Oaks New Jersey amber; Turonian, est. 94-90 mya) was considered by its authors to be a "ponerine". The term "poneromorph" is appropriate, since the former subfamily Ponerinae now comprises 6 modern poneromorph subfamilies. No assessment is given as to whether the 4th

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[4] In modern poneromorphs the postpetiole is not usually strongly constricted posteriorly to form a distinct node, but poneromorphs are engineered for postpetiolar development because of their tubulate 4th abdominal exoskeleton and its insertion into the 3rd segment. A few poneromorphs are quite strongly postpetiolate, including *Paraponera* (Paraponerinae) and some species of *Cerapachys* (Cerapachyinae) and *Proceratium* (Proceratiinae).

abdominal segment is tubulate or not. Such indication is required if fossils are claimed to be poneromorph. Constriction of the 4th abdominal segment alone is insufficient for confident identification – the defining character is the presence of its tubular structure. That said, the published *Brownimecia* illustrations do evidence tubulation. Bolton (2003) placed *Brownimecia* in a monotypic subfamily Brownimeciinae, and considered that "It may belong, speculatively, in a basal group that is sister to the poneromorphs, or perhaps to the poneromorphs and leptanillomorphs together". Both of these subfamily groups have tubulate abdomens, and many species are postpetiolate.

Canopone dentata Dlussky (1999)(Medicine Hat, Alberta; Campanian, late Cretaceous, est. 83.5 – 70.6 mya) has a clearly tubulate abdomen and somewhat constricted postpetiole. Dlussky was unsure of its placement as a "ponerine" or myrmeciine. I consider it to be poneromorph, with some similarities to *Paraponera.* The presence of worker ocelli is unusual in poneromorphs, but that character is present in living *Harpegnathos*.

A posteriorly constricted postpetiolar node is present in *Afromyrma* Dlussky, Brothers and Rasnitsyn (2004)(Orapa, Botswana; Turonian, est. 94-90 mya). Its compression fossil is poorly preserved but seems certainly to be myrmicomorph. Its was originally assigned to subfamily Myrmicinae.

Eotapinoma macalpinei Dlussky (1999) from Canadian amber (Medicine Hat, Alberta; Campanian, late Cretaceous, est. 83.5 – 70.6 mya) was considered a likely dolichoderine by its author and a "putative dolichoderine" by Grimaldi and Agosti (2000b).

Gerontoformica cretacica Nel, Perrault, Perrichot and Neraudeau (2004)(Archingeay-les-Nouillers, Charente-Maritime, SW France; Uppermost Albian amber, est. 100 mya) is not well preserved, but the published photographs of its petiole and gaster closely recall *Nothomyrmecia*. Nothing in the original paper challenges this resemblance. *Gerontoformica* is described as having peg-like teeth on its clypeus (reminiscent of Amblyoponinae and Anomalomyrmini (Leptanillinae)), small eyes and long mandibles. Its authors remarked that its first gastral (i.e. 3rd true abdominal) segment had a "pretergite", though their fig 2c seems to illustrate this character for the 4th abdominal segment. They did not indicate whether abdominal segment 4 was tubulate or not, but their photographs imply the latter. The fossil was said to lack a sting, but Fig. 2a, seems to depict an unexserted sting shaft. Fig. 1c does not represent the head in detail sufficient to illustrate the textural description of cephalic, mandibular and antennal particulars. The discovery of more specimens from Archingeay is eagerly awaited. The authors are urged to publish line illustrations backing-up their observations and photographs.

Using Bayesian dating analysis Ward and Brady (2003) indicate that the most recent common ancestor of a clade containing *Nothomyrmecia* and *Myrmecia* is 74 my old (95% confidence limits 53-101my).

Derivation of the several living dorylomorph army ant subfamilies from ancestral stock considered antecedent also to the Cerapachyinae has recently been rigorously estimated to have occurred in mid Cretaceous times (i.e. around 100mya), possibly in Gondwana (Brady, 2003), providing further evidence that true ants of modern appearance and taxonomic affinity, with behavior like that of highly specialized modern ants, were likely present by the late Cretaceous

These examples all imply that evolution from solitary wasp ancestry to ant eusociality could have been complete within the first few million years of formicid history, with tens of millions of years available to play out the details, including the extinction of non-eusocial formicids, which probably disappeared promptly anyway following the rise of eusocial ant competitors. It also seems likely that the earliest events in formicid evolution would have occurred within a limited geographical range, perhaps entirely in Gondwana or one of its drifting continental fragments, so the loss of groups standing as sister taxa to those of the emerging main formicid lineage would have been local geographical events.

It appears that mid-Cretaceous aculeates would have included a cluster of related lineages among which the prospective formicid synapomorphies first evolved and began successively to accumulate. At the point of each character acquisition two sister taxa would be generated, one lacking the new character, but possessing those previously evolved. There would probably at times have been several contemporaneous taxa carrying incomplete sets of the relevant characters. Also, some of the characters could have arisen more than once, later to be secured as potential formicid synapomorphies by the surviving lineage. One lineage alone, according to this model, followed the course prescribed here and that lineage is represented today only by the living ants – the remaining taxa significant to this history have in the meantime become extinct.

It also appears *prima facie* that the fossil record has not yet yielded possible pre-eusocial ant ancestors with incomplete sets of the relevant characters reviewed above. The hypothecated first solitary protoformicid would be a strong candidate for recognition as a fossil. It would probably have the general facies of a modern solitary vespid wasp, with metapleural glands or antecedent structures, but probably not a petiolar waist node or elbowed antennae (though many modern solitary vespids have somewhat elongated scapes). A fossilized dealate, queen-coeval forager from an ancestral semisocial formicid colony of the type posited here would probably have a more generally (perhaps substantially) ant-like facies but with some wasp-like attributes. It would very likely be identified as a somewhat wasp-like dealate female eusocial ant, unless its fossilization preceded acquisition of the petiolar node and/or elbowed antennae, or it had those characters incompletely developed compared to modern ants. The extinct subfamily Armaniinae Dlussky (reviewed by Bolton, 2003: 73, 259) requires consideration in these regards (P.S.

What is *Sphecomyrma*?

The extinct genus *Sphecomyrma* (type species *S. freyi* Wilson, Carpenter and Brown, 1967) was based on two worker specimens enclosed in a piece of Turonian New Jersey amber of estimated age 92 mya. Its characteristics are summarized in the original paper, and by Grimaldi, Agosti and Carpenter (1997). They will not be reiterated here.

Further specimens from New Jersey are now known (of Turonian age, mid Cretaceous, ca 92 mya. – Grimaldi, Agosti and Carpenter, 1997). A second closely similar worker-based species *S. canadensis* Wilson has been described from Alberta, Canada (78-79 mya), and a worker-based related genus *Cretomyrma* Dlussky from the Taymyr peninsula, Siberia (of Santonian age, 85.5-83.5 mya). Two male-based genera *Dluskyidris* Bolton and *Baikuidris* Dlussky (both from Siberian Santonian amber) are believed to be relatives of *Sphecomyrma*. All are currently classified in family Formicidae, subfamily Sphecomyrminae. There have been no reports of fossil alate or dealate females.

Sphecomyrma has also been reported from late Albian Burmese amber (ca 100-105 mya)(Grimaldi, Engel and Nascimbene, 2002), along with an enigmatic poneroid fossil which represents the oldest known definitive ant. A further new species has recently been discovered in New Jersey amber (Engel and Grimaldi, in prep.). These authors will report multiple workers of *S. freyi* from a single piece of New Jersey amber, implying that the species was social. Engel (pers com.) “would argue that *Sphecomyrma* was a likely social (perhaps even eusocial) early group of ants”, a view with which I concur.

There has been much discussion concerning the taxonomic and phylogenetic status of *Sphecomyrma*. It has been considered a taxon sister to the Formicidae, with the two families comprising superfamily Formicoidea (Wilson, Carpenter and Brown,1967), assigned with the other taxa indicated above to subfamily Sphecomyrminae in family Formicidae (Grimaldi, Agosti and Carpenter, 1977; Bolton, 2003), or alleged perhaps not to be an ant at all, and to require a separate family (Dlussky, 1975, and his other references in Grimaldi, Agosti and Carpenter 1997). Baroni Urbani in 1988 considered it to be a nonsocial wasp (reported in Grimaldi and Agosti, 2000b). In the morphological phylogenetic analysis of Ward and Brady (2003) *Sphecomyrma* is sister to the extant ants sampled, with strong bootstrap support.

The argument centers on whether or not the relevant fossils possess metapleural glands (which were identified with reservation in the original Wilson, Carpenter and Brown paper). Recent researchers using recently collected specimens agree that metapleural glands are present, and the affirmative evidence of Grimaldi, Agosti and Carpenter (1997) is convincing. It has also been suggested that the antennae, which have shorter scapes than in all living female ants, could indicate that *Sphecomyrma* might be neither eusocial nor an ant (see Grimaldi, Agosti and Carpenter (1997) for summary). The last hypothesis is probably unfalsifiable.

Wilson (1971: 31) considered the wasp-like mandibles of *Sphecomyrma* an anomaly in comparison with the very different mandibles of *Amblyopone*, which was presented as an archetypical primitive ant. This difficulty is resolved by the model for ant evolution presented here. It envisages a range of mandibular specializations among the hypothecated semisocial formicids, easily accommodating both *Sphecomyrma* and *Amblyopone*. Note that broadly "wasp-like" mandibles are present in virtually all male ants, despite the great range of mandibular specializations seen among ant workers.

At the risk of introducing a further probably unfalsifiable hypothesis, I represent that the various *Sphecomyma* fossils could be females or workers of a semisocial formicid, like those hypothecated here.

It was suggested above that these insects would likely have retained strong wasp-like characteristics along with emerging resemblances to modern ants, that ocelli would be present, and that the antennae and waist nodes in some species might have transitional rather than fully ant-like structure. Also that some species might either (1) like mutillids, have evolved monomorphic wingless females with mesosomal reductions homoplasiously resembling those of modern worker ants, or (2) have evolved a eusocial-ant-like apterous worker caste while retaining standard reproductives (the two castes being congenerational within nests). All these possibilities are plausible, and all could apply to *Sphecomyrma*. It could represent a species meeting either of the two options numbered above.

Those interested in this proposition should consider it while re-reading the classic Wilson, Carpenter and Brown paper. Its authors believed *Sphecomyrma* to be "truly intermediate between primitive ants and the aculeate wasps" and stated that "if we are mistaken about the presence of the metapleural gland, it would be possible to consider *Sphecomyrma* a wasp rather than an ant". In other words they considered the metapleural glands to be essentially the only definitively formicid attribute of *S. freyi*.

Such observations regarding wasp/ant intermediacy would also apply exactly to the semisocial formicids hypothecated here.

The "true" nature of *Sphecomyrma* might in fact be intractable because either: (1) the discovery of alate or dealate female *Sphecomyrma* fossils would not falsify the above hypothesis, since they could be related semisocial formicids of another species which had not lost flight capacity. Neither would they prove that the *Sphecomyrma* fossils were eusocial workers; or (2) alate or dealate fossils with "complete" mesosomal structure, collected in indubitable conspecific association with mesosomally-reduced specimens like the known *Sphecomyrma* fossils, could represent *either* a semisocial species with congenerational alate/dealate females and apterous workers, *or* a fully eusocial ant with apterous mesosomally-reduced daughter workers. They would indicate at best *only* that *Sphecomyrma* was *either* a semisocial *or* a eusocial formicid.

The mesosoma in *Sphecomyrma* is unusual compared to those of all modern ants, but the suggestion by Wilson, Carpenter and Brown (1967) that the suture between the meso- and metathorax is “possibly movable” seems implausible.

Concluding remarks

Past discussions on the origins and evolution of formicid eusociality have reiterated the Wheeler/Malyshev hypothesis (Wheeler, 1928: 63; Malyshev, 1968). It was reviewed without significant support by Wilson (1971) and Hölldobler and Wilson (1990), and will not be further considered here. Wilson’s suggestion (1971) that amblyoponine ants might have evolved in the Wheeler/Malyshev manner via *Scleroderma*-like ancestry is untenable (Hölldobler and Wilson, 1990).

Various authors, notably Wilson (1971: 72), Hölldobler and Wilson (1990: 27) and Bourke and Franks (1995: 73) have espoused the “subsocial route” for evolution of ant eusociality, largely inspired by the seminal analysis of wasp sociality by Evans (1958). This model derives formicid eusociality ultimately from groups comprising a parental female caring for her nondispersing daughters. The model implies that such ancestral females would have initiated their colonies alone, not in pleometrotic foundress groups. It is argued that this is the usual mode of development of modern ant colonies, which is held in effect to reflect phylogeny and to support the model. It is also held that semisocial groups of the kind posited in this essay would lack kinship bonds sufficient for the semisocial model to operate under natural selection. Bourke and Franks considered the semisocial option “a poor model for the origin of altruism in early ants”.

The first assumption is simplistic. Pleometrotic colony foundation by partially claustral groups of coeval mated females could just as well be homologous with the ancestral condition, as proposed above. Pleometrosis is known largely among “primitive” ants (Wheeler, 1933, Wilson, 1971, Hölldobler and Taylor, 1983), and its general absence in “higher” ants, *versus* solitary colony foundation, could reflect a phylogenetic succession.

The ability of queens to found colonies alone without foraging is another feature of ants based on the presence of allectomy, which provided the opportunity for metabolization of the redundant post-dealation flight muscles in order to sustain claustral, solitary foundress females and their initial brood. The larvae in such founding colonies are fed by the queen with surplus eggs, or trophic egg material, or nutrient provided by trophallaxis (processes broadly analogous with milk feeding in mammals, by which female biomass is converted to larval biomass).

Solitary, claustral colony foundation is in fact commonly practiced mainly among the formicomorph and myrmicomorph subfamilies. Their queens are usually much larger than conspecific workers. The myrmeciomorphs, many poneromorphs and several known myrmicines, are partially claustral, frequently with pleometrosis (see Wilson, 1971:

72). The dorylomorphs and leptanillomorphs (possibly excluding the barely studied Anomalomyrmini and a few cerapachyines) and some other "army ants", like *Onychomyrmex* (Amblyoponinae), have apterous queens and found new colonies by budding, as do those Ectatomminae, Heteroponerinae and Ponerinae with apterous reproductives or gamergates. Most of these, except the dorylomorph and leptanillomorph army ants, have relatively small queens, little larger than workers. Solitary foundation is thus broadly correlated with the secondary presence of strong size dimorphism between flying queens and their workers, where the ratio of available bulk of maternal mesosomal flight musculature to biomass of the foundation brood is high. It cannot be represented as the likely situation in the earliest formicids.

The initial groups of winged communal wasps posited in the current model would draw their personnel from local populations, so would likely have significant relationship ties. Natural selection would work upon such groups whatever their composition, and if individuals joining positively selected groups were more likely than non-joiners to reproduce, their group-joining behavior would be positively selected. Note that, in the earliest stages of group formation discussed above, all joiners would have the opportunity to contribute eggs to the collective cache, and their average chances for survival and reproduction could be better than if they had not joined. Even if some individuals lost out in the reproductive stakes the group could still be relatively adaptive, and the tendency by mated females to join groups could become selectively established. Furthermore, if those groups with the most closely related personnel tended to be the best survivors, selection would favor individuals which grouped with close relatives such as sisters. This process could furnish the allegedly deficient kinship bonds.

Wheeler (1928: 107) considered that "The Ponerinae represent the primitive stock from which the other ant subfamilies…have radiated". He asked "Are the various subfamilies of ants really derived from a common stock or are they polyphyletic like the various social subfamilies of wasps and bees?" Careful reading indicates that he was talking about the "various subfamilies of ants" as possible *separate social lineages*. He answered (p. 108) "I deem it…probable...that the family (*i.e. the Formicidae as a social lineage*) as a whole is monophyletic".

In reaching that conclusion Wheeler specifically rejected a phylogenetic scheme diagrammatically proposed by Emery (1920: 370; the diagram reproduced by Wheeler, 1928: 107). This posited several lines of evolution from an "unknown hypothetical formicid stock" out of which the following lineages were derived: (1) a "Prodorylinae" (*i.e. Cerapachyinae*) – Dorylinae line, (2) a line comprising a hypothetical ancestral group the "Proponerinae", (3) a lineage labeled "?Dolichoderinae", and (4) a lineage labeled "?Formicinae". The "Proponerinae" gave rise to several lines labeled: (1) Euponerinae; (2) Amblyoponini, Ectatommini, Proceratiini; (3) Myrmeciini, Platythyreini; and (4) Myrmicinae. Wheeler expressed the view that this model "indicated a polyphyletic origin of the subfamilies", and that was his main reason for rejecting it. Emery's proposal was ultimately monophyletic, in that he clearly considered the hypothetical stock to have been monophyletic, but it is not clear whether he considered the lineages he depicted to have represented separate origins of sociality as Wheeler concluded.

Emery's phylogenetic concept was in fact structurally close to that proposed here. His "unknown hypothetical formicid stock" is schematically equivalent to the semisocial formicids of the current model (and his "Proponerinae" is close to the "poneroid lineage" of Brown; 1954).

Wheeler (p. 108) rejected Emery's model because: "if we take Emery's point of view…the hypothetical ancestors must have been very primitive and in all probability solitary or subsocial Aculeates". Thus Emery and Wheeler between them, came close to the phylogenetic hypothesis developed in this essay (even though the latter opted for the subsocial route). A shift of emphasis by Wheeler almost 80 years ago might have generated ideas similar to those expressed here. Ideas, like evolution, can be very chancy!

The early stages of the evolutionary path to formicid eusociality proposed above relate well to the "polygynous family hypothesis" of West-Eberhard (1978). The presence of allectomy, however, projected the ant lineage on a later course completely different from those of other socially advanced aculeates. The fact that the simple act of dealation can determine the potential for future worker versus reproductive status in female ants provided a mechanism for ready establishment of the worker caste and eusociality. That is the most important component of this model!

Several recent studies have investigated the internal phylogeny of family Formicidae cladistically, or by DNA sequence analysis and comparison, most notably Baroni Urbani, Bolton and Ward (1992); Shattuck (1992); Grimaldi, Agosti and Carpenter (1997); Grimaldi and Agosti (2000a), Brady (2003); Ward and Brady (2003); and Saux et al. (2004). More work in this area is desirable, especially with the possibility of multiple evolution of eusociality in mind. Possibly significant worker mesosomal and postpetiolar characters need to be better understood, along with features related to the many pheromone-producing glands of ants, especially those involved in the laying of scent trails. Further work on proventricular structure, especially in the poneromorph, dorylomorph, leptanillomorph and myrmicomorph subfamilies might yield phylogenetically useful characters.

There is a degree of prospective adaptation at each phylogenetic level in the model proposed here. It is almost as if each step was automatically destined to be followed by the next. This is especially true of the semisocial formicids with colonies comprising dealate reproductive females and workers of one generation, and alate, potentially reproductive, females of the next. Evolution of a eusocial worker caste following premature dealation of daughter alates in the manner described above is so simple a process that its occurrence could be considered almost predictable. Perhaps this should not amaze hymenopterists, for the various major groups of aculeates have produced many separate social lineages, with a number culminating in eusociality (in several groups of bees, vespine wasps, a sphecoid wasp and ants). This must have been, in effect, preordained by the unique set of relevant characteristics phylogenetically assembled in the ancestor common to all of these taxa.

Whether or not this model is considered plausible, it is clear that ants as aculeates are endowed with a number of extraordinary characteristics. They have metapleural glands, allectomy in alate reproductive females, permanently apterous workers and strong worker dimorphism, often with large-headed soldiers; they lay scent trails, have acellular nests, and may practice nocturnal and/or hypogaeic foraging behavior. In each case these characteristics are unique to ants or very unusual, even rare, among other aculeates.

In conclusion ants, as my title implies, are very strange wasps indeed!

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